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New species of Cretaceous Locustopsidae (Orthoptera: Caelifera) from the Crato Formation of Brazil and a taxonomic revision of the family

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Abstract

A new genus and four new species of Locustopsidae Handlirsch, 1906 are described from the Crato Formation of northeastern Brazil. *Aestuacrida stereofemoris* **gen. et sp. nov.** differs from previous genera of the family by having four branches of CuA + CuPaα. A new species of *Araripelocusta* Martins-Neto, 1995, *Araripelocusta imperatrix* **sp. nov.**, is much larger than previous congeners with a wingspan of ca. 39 mm and features two little leaf-like appendages on the dorsal front part of the head. *Parapleurites brasiliensis* **sp. nov.** is the first Cretaceous member of this genus following two Jurassic predecessors. *Parapleurites morrisonensis* Smith, Gorman, Pardo & Small, 2011 has a wing venation that more closely resembles *Mesolocustopsis* Hong and Wang, 1990 and is moved to this genus as *M. morrisonensis* **comb. nov.** *Cratolocustopsis aquila* **sp. nov.** joins *C. cretacea* (Martins-Neto, 1990) and *C. contumax* Martins-Neto, 2003 as the third member of this genus, helping to solidify its separate position from other genera of Locustopsidae. A comprehensive taxonomic revision of all known species of Locustopsidae is given to improve our understanding of the diversity of these short-horned Mesozoic grasshoppers. The genus *Cratozeunerella* Martins-Neto, 1998 is considered a junior synonym of *Zeunerella* Sharov, 1968. *Cratozeunerella godoii* Martins-Neto, 2003, *C. nervosa* Martins-Neto, 2003, *C. soaresi* Martins-Neto, 2003 and *C. titanella* Martins-Neto, 2003 are suggested to be included in *Locustopsis* Handlirsch, 1906. *Plesioschwinzia* Zessin, 1988 is considered a junior synonym of *Locustopsis*. Further changes on the species level concern former *Zeunerella reticulata* (Handlirsch, 1939) which is moved to *Cratolocustopsis* Martins-Neto, 2003. *Mesolocustopsis petruleviciusi* (Martins-Neto, 2003) is considered a junior synonym of *M. caririensis* (Martins-Neto, 1990). In *Locustopsis* two synonyms are proposed: *Locustopsis elongata* Handlirsch, 1906 **syn. nov.** of *L. elegans* Handlirsch, 1906, and *Locustopsis lacera* (Zessin, 1983) (former *Plesioschwinzia lacera*) **syn. nov.** of *L. gyra* Zessin, 1983. Additionally, *Locustopsis anatolica* Sharov, 1968 is moved to *Schwinzia* Zessin, 1983. The recently described species of the Chinese *Sinolocustopsis* Huang & Nel, 2024 are moved to the genus *Locustopsis*: *Locustopsis elongatus* **comb. nov.** (Huang & Nel, 2024) and the genus *Mesolocustopsis*: *Mesolocustopsis brevis* **comb. nov.** (Huang & Nel, 2024). *Liadolocusta auscultans* Handlirsch, 1906 is considered a *nomen nudum*. *Locustopsites gigantea* Théobald, 1937 is probably a member of Tettigoniidae Krauss, 1902 and should be excluded from Locustopsidae.

Key words: Araripe Basin, Lower Cretaceous, fossil grasshoppers, Konservat-Lagerstätte

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Introduction

Locustopsidae Handlirsch, 1906 represents an extinct clade of Caelifera Ander, 1936, nested within Acridomorpha Macleay, 1821. Despite its longstanding recognition, the monophyly of Locustopsidae remains questionable due to the absence of unambiguous apomorphies defining the group (Nel & Jouault, 2022). Nonetheless, the family is traditionally distinguished from other fossil Orthoptera Olivier, 1789 by a combination of wing venation features: the CuA + CuPaα, M, and RP remain distinct, unconnected by pseudo cross veins-contrasting with the (presumably) closely related Locustavidae Sharov, 1968, in which these veins are proximally fused by such pseudo cross veins. Also, Locustopsidae have a single main branch of RA and an elongated ScP reaching near the wing apex (with exception of *Locustrix* Martins-Neto, 2003, which exhibits a reduced ScP).

The family currently comprises two subfamilies—Araripelocustinae Martins-Neto, 1995 and Locustopsinae Handlirsch, 1906—as well as a set of genera of uncertain subfamilial affinity (Cigliano *et al.*, 2025). Araripelocustinae, characterized by a single M branch in the tegmina, includes *Araripelocusta* Martins-Neto, 1995 from the Crato Formation (Brazil) and *Britannacrida* Gorochov, Jarzembowski & Coram, 2006 from the Lower Cretaceous beds of Dorset (UK) (Gorochov *et al.*, 2006). In contrast, Locustopsinae are characterized by featuring multiple branches of M (two or three), including *Orichalcum* Whalley, 1985—taxonomically ambiguous due to its fused M and RP veins resembling the ensiferan Elcanidae Handlirsch, 1906—and *Conocephalella* Strand, 1926, which remains poorly known since its original description (Deichmüller, 1886).

The remaining genera of Locustopsinae are broadly distributed across Jurassic and Cretaceous localities in Europe (UK, Germany), Asia (China), Africa (Egypt), and the Americas (Brazil, USA), as documented in formations such as Jiulongshan, Morrison, and Crato (Tab. 1) (Ansorge, 1991; Gorochov & Coram, 2023; Gu *et al.*, 2016; Martins-Neto, 2003; Smith *et al.*, 2011; Zessin, 1983). Their taxonomy relies primarily on the number and arrangement of M and CuA + CuPaα branches, especially the relative positions of MA1, MA2, and MP (Tab. 2) (Gorochov *et al.*, 2006). The genus *Plesioschwinzia* Zessin, 1988 is very similar to *Locustopsis*. In fact, the genera are separated only by the number of branches of ScP (1–4 in *Plesioschwinzia*, 6–8 in *Locustopsis*) (Gorochov & Coram, 2023).

Some genera remain unplaced within either subfamily due to incomplete or atypical material. *Liadolocusta* Handlirsch, 1906 is known solely from a foreleg, while *Locustopsites* Théobald, 1937 was described on a possibly overlapping pair of forewings with tettigoniid-like venation (pers. comm. O. Béthoux). *Locustrix* resembles *Cratolocustopsis* Martins-Neto, 2003 in M and CuA + CuPaα branching (i.e., two), but differs in its shorter ScP, which extends only halfway along the wing (Martins-Neto, 2003). *Pseudoacrida* Lin, 1982 is distinguished by a tegminal CuA + CuPaα that extends beyond its connection with CuPaβ as a separate branch of CuA. More recently, *Sinolocustopsis* Nel & Huang, 2024, described from the Middle Jurassic of China, displays a forewing venation similar to *Locustopsis*, with three M, MA2 in direct contact to MA1, and two CuA + CuPaα branches.

The Crato Formation, a Lower Cretaceous Koservat-Lagerstätte in northeastern Brazil, is a major source of well-preserved fossil orthopterans. As of July 2024, the Locustopsidae are represented by 19 valid species across seven genera in this unit, making them the second most diverse orthopteran group in the formation after Baissogryllidae Gorochov, 1985 (20 spp. (Cigliano *et al.*, 2025) (Tab. 1)). Other orthopteran families from Crato include Gryllidae Laicharting, 1781 (13 spp.), and several with much lower diversity (compared to Baissogryllidae and Locustopsidae) such as Tridactylidae Brullé, 1835, Proscopiidae Serville, 1838, Prophalangopsidae Kirby, 1906, Gryllotalpidae Leach, 1815, Elcanidae Handlirsch, 1906, and Bouretidae Martins-Neto, 2001, each with one to three known species (Cigliano *et al.*, 2025; Mendes *et al.*, 2019; de Moura-Júnior *et al.*, 2018; Nel & Jouault, 2022).

In this study, we describe a new genus and four new species of Locustopsidae from the Lower Cretaceous deposits of the Crato Formation, Brazil. These taxa contribute to our understanding of the morphological diversity and taxonomic boundaries of the family. A critical reassessment of the diagnostic criteria and subfamily placements within Locustopsidae is also provided, aiming to refine the taxonomy of this lineage of extinct Orthoptera.

TABLE 1. Species of Locustopsidae Handlirsch, 1906, their geographical origin, and associated era. Due to their uncertain/misidentified taxonomic status *Liadolocusta auscultans* Handlirsch, 1906, *Conocephalella capito* (Deichmüller, 1886) and *Locustopsites gigantea* Théobald, 1937 are excluded. Locality information from Cigliano *et al.*, 2025 and Paleobiology Database (https://paleobiodb.org/#/, 25.10.2024).

Species	Publication	Locality	Era
Parapleurites morrisonensis	Smith, Gorman, Pardo & Small, 2011	USA/Morrison Formation	Upper Jurassic
Araripelocusta brevis	Martins-Neto, 1995	Brazil/Crato Formation	Lower Cretaceous
Araripelocusta longinota	Martins-Neto, 1995	Brazil/Crato Formation	Lower Cretaceous
Cratolocustopsis contumax	Martins-Neto, 2003	Brazil/Crato Formation	Lower Cretaceous
Cratolocustopsis cretacea	(Martins-Neto, 1990)	Brazil/Crato Formation	Lower Cretaceous
Cratozeunerella amedegnatoi	Martins-Neto, 1998	Brazil/Crato Formation	Lower Cretaceous
Cratozeunerella godoii	Martins-Neto, 2003	Brazil/Crato Formation	Lower Cretaceous
Cratozeunerella neotropica	Martins-Neto, 1998	Brazil/Crato Formation	Lower Cretaceous
Cratozeunerella nervosa	Martins-Neto, 2003	Brazil/Crato Formation	Lower Cretaceous
Cratozeunerella soaresi	Martins-Neto, 2003	Brazil/Crato Formation	Lower Cretaceous
Cratozeunerella titanella	Martins-Neto, 2003	Brazil/Crato Formation	Lower Cretaceous
Mesolocustopsis araripensis	(Martins-Neto, 1990)	Brazil/Crato Formation	Lower Cretaceous
Mesolocustopsis caririensis	(Martins-Neto, 1990)	Brazil/Crato Formation	Lower Cretaceous
Mesolocustopsis petruleviciusi	(Martins-Neto, 2003)	Brazil/Crato Formation	Lower Cretaceous
Mesolocustopsis vikingi	(Martins-Neto, 2003)	Brazil/Crato Formation	Lower Cretaceous
Zessinia pulcherrima	Martins-Neto, 1990	Brazil/Crato Formation	Lower Cretaceous
Zessinia reticulata	Martins-Neto, 1990	Brazil/Crato Formation	Lower Cretaceous
Locustrix audax	Martins-Neto, 2003	Brazil/Crato Formation	Lower Cretaceous
Locustrix gallegoi	Martins-Neto, 2003	Brazil/Crato Formation	Lower Cretaceous
Pseudoacrida sennlaubi	Nel & Jouault, 2022	Brazil/Crato Formation	Lower Cretaceous
Britannacrida distincta	Gorochov, Jarzembowski & Coram, 2006	UK/Lulworth Formation	Lower Cretaceous
Locustopsis posterior	Gorochov, Jarzembowski & Coram, 2006	UK/Lower Purbeck	Lower Cretaceous
Mesolocustopsis anglica	Gorochov, Jarzembowski & Coram, 2006	UK/Durlston Formation	Lower Cretaceous
Mesolocustopsis angusta	Gorochov, Jarzembowski & Coram, 2006	UK/Weald Clay Formation	Lower Cretaceous
Mesolocustopsis problematica	Gorochov, Jarzembowski & Coram, 2006	UK/Weald Clay Formation	Lower Cretaceous
Zessinia borealis	Gorochov, Jarzembowski & Coram, 2006	UK/Lulworth Formation	Lower Cretaceous
Zeunerella prior	Gorochov, Jarzembowski & Coram, 2006	UK/Weald Clay Formation	Lower Cretaceous
Locustopsis brodiei	Cockerell, 1916	UK/Binton	Lower Jurassic
Locustopsis bucklandi	(Brodie, 1845)	UK/Grafton	Lower Jurassic
Locustopsis cockerelli	Handlirsch, 1939	UK/Binton	Lower Jurassic
Orichalcum ornatum	Whalley, 1985	UK/Shales with Beef Formation	Lower Jurassic
Plesioschwinzia lacoei	(Cockerell, 1916)	UK/Binton	Lower Jurassic
Plesioschwinzia uvarovi	(Zeuner, 1942)	UK/unknown	Lower Jurassic
Locustopsis constricta	Zeuner, 1942	UK/Lilstock Formation	Upper Triassic
Locustopsis cubitalis	Zeuner, 1942	UK/Lilstock Formation	Upper Triassic
Locustopsis spectabilis	Zeuner, 1942	UK/Lilstock Formation	Upper Triassic
Plesioschwinzia gracilis	(Zeuner, 1942)	UK/Lilstock Formation	Upper Triassic

.....continued on the next page

TABLE 1. (Continued)

Species	Publication	Locality	Era
Plesioschwinzia sharovi	Gorochov & Coram, 2023	UK/Lilstock Formation	Upper Triassic
Locustopsis dubia	Handlirsch, 1939	Germany/Dobbertin	Lower Jurassic
Locustopsis elegans	Handlirsch, 1906	Germany/Dobbertin	Lower Jurassic
Locustopsis elongata	Handlirsch, 1906	Germany/Dobbertin	Lower Jurassic
Locustopsis gyra	Zessin, 1983	Germany/Dobbertin	Lower Jurassic
Locustopsis maculosa	Bode, 1953	Germany/Posidonia Shale Formation	Lower Jurassic
Locustopsis nana	Handlirsch, 1939	Germany/Dobbertin	Lower Jurassic
Locustopsis pulchella	Zessin, 1983	Germany/Dobbertin	Lower Jurassic
Locustopsis reducta	Handlirsch, 1939	Germany/Dobbertin	Lower Jurassic
Locustopsis sippeli	Zessin, 1983	Germany/Lehmhagen	Lower Jurassic
Plesioschwinzia bernstorffi	(Geinitz, 1880)	Germany/Dobbertin	Lower Jurassic
Plesioschwinzia kruegeri	(Zessin, 1983)	Germany/Schandelah	Lower Jurassic
Plesioschwinzia lacera	(Zessin, 1983)	Germany/Dobbertin	Lower Jurassic
Plesioschwinzia procera	(Zessin, 1983)	Germany/Dobbertin	Lower Jurassic
Plesioschwinzia thalassophila	Zessin, 1988	Germany/Dobbertin	Lower Jurassic
Schwinzia sola	Zessin, 1983	Germany/Dobbertin	Lower Jurassic
Zeunerella mecklenburgica	(Zessin, 1983)	Germany/Dobbertin	Lower Jurassic
Zeunerella reticulata	(Handlirsch, 1939)	Germany/Dobbertin	Lower Jurassic
Locustopsis germari	(Münster, 1842)	Germany/Solnhofen Formation	Upper Jurassic
Locustopsis africanus	Ansorge, 1991	Egypt/Tonsteinserie Formation	Lower Cretaceous
Locustopsis anatolica	Sharov, 1968	Kyrgyzstan/Dzhil Formation	Lower Jurassic
Locustopsis karatavica	Sharov, 1968	Kazakhstan/Karabastau Formation	Upper Jurassic
Zeunerella arborea	Sharov, 1968	Kazakhstan/Kzyl-Zhar	Upper Cretaceous
Locustopsis apicalis	Zherikhin, 1985	Siberia/Itat Formation	Lower Jurassic
Locustopsis picta	Zherikhin, 1985	Siberia/Itat Formation	Lower Jurassic
Locustopsis ferghanensis	Martynov, 1937	Kyrgyzstan/Sulyukta Formation	Lower Jurassic
Locustopsis shurabica	Sharov, 1968	Kyrgyzstan/Sagul Formation	Lower Jurassic
Parapleurites gracilis	Brauer, Redtenbacher & Ganglbauer, 1889	Siberia/Cheremkhovskaya Formation	Lower Jurassic
Parapleurites sibiricus	Sharov, 1968	Siberia/Cheremkhovskaya Formation	Middle Jurassic
Mesolocustopsis sinica	Hong & Wang, 1990	China/Laiyang Formation	Lower Cretaceous
Pseudoacrida costata	Lin, 1982	China/Liupanshan Basin	Lower Cretaceous
Locustopsis rhytofemoralis	Gu, Yue, Shi, Tan & Ren, 2016	China/Jiulongshan Formation	Middle Jurassic
Sinolocustopsis elongatus	Nel & Huang, 2024	China/Yan'an Formation	Middle Jurassic
Sinolocustopsis brevis	Nel & Huang, 2024	China/Yan'an Formation	Middle Jurassic

TABLE 2. Generic separation of Locustopsidae Handlirsch, 1906 on the basis of wing venation. Missing are *Liadolocusta* Handlirsch, 1906 and *Conocephalella* Strand, 1926 because they are insufficiently known to be included in a comparison and *Locustopsites* Théobald, 1937 because it probably does not belong in Locustopsidae.

Genus	Branches of CuA + CuPaα	Branches of M	Contact of MA2	Separating character from similar genus
Araripelocusta Martins-Neto, 1995	1	1	-	-
Britannacrida Gorochov, Jarzembowski & Coram, 2006	2	1	-	-
Cratolocustopsis Martins-Neto, 2003	2	2	-	-
Locustrix Martins-Neto, 2003	2	2	-	ScP markedly shorter, ca. 50% of total wing length
Cratozeunerella Martins-Neto, 1998	2	3	MP	ScP with many cross veins
Zeunerella Sharov, 1968	2	3	MP	ScP without cross veins
Locustopsis Handlirsch, 1906	2	3	MA1	ScP with 6–8 branches
Sinolocustopsis Nel & Huang, 2024	1–2	3	MA1	ScP with 2–3 branches
Plesioschwinzia Zessin, 1988	2	3	MA1	ScP with 1–4 branches
Orichalcum Whalley, 1985	2	3	MA1	M and RP fused to one branch
Mesolocustopsis Hong & Wang, 1990	1	3	MA1	CuA + CuPaα does not continue past fusion to CuPaβ
Pseudoacrida Lin, 1982	1	3	MA1	CuA + CuPaα continues past fusion to CuPaβ as separate CuA
Zessinia Martins-Neto, 1990	1	3	MP	-
Parapleurites Brauer, Redtenbacher & Ganglbaer, 1889	3	2	-	-
Schwinzia Zessin, 1983	3	3	MA1	-

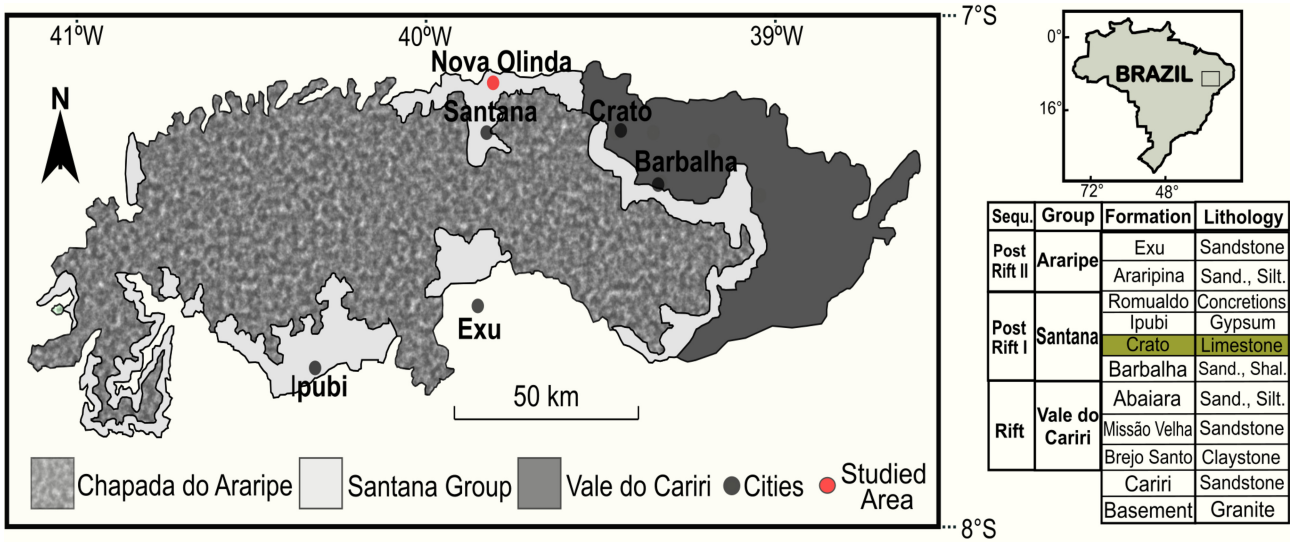
Geological Setting

Fig. 1

The break-up of Africa and South America led to the formation of several hinterland basins in Brazil during the Jurassic-Cretaceous interval. The Araripe Basin is the largest and most complete basin in the interior of northeastern Brazil, being one of the most prominent examples of this phase (Assine, 2007). The sedimentary history of this basin is linked to rifting processes and can be divided into pre-rift, rift, and post-rift tectonic sequences (Ponte and Ponte Filho, 1996). The post-rift tectonic sequence is divided into two events: the post-rift I and post-rift II (Assine *et al.*, 2014). The post-rift I is represented from base to top by the Barbalha, Crato, Ipubi, and Romualdo formations, stacked within the Santana Group (Assine *et al.*, 2014).

The Crato Formation is characterized by lacustrine carbonates, which are interlayered, at least at its top, by green shales and fine-to-coarse sandstones (Santos *et al.*, 2017). The carbonates of the Crato Formation can be distinguished into six informal layers (C1–C6), of which C6 at the top of the formation is exposed in quarries near Nova Olinda and Santana do Cariri, Ceará State (Neumann *et al.*, 2003) (Fig. 1). Crato limestones are famous for their abundance of high-quality fossils. The excellent preservation of Crato fossils have made it known worldwide

as a Fossil Konservat-Lagerstätte. This Lagerstätte is a para-autochthonous to allochthonous assemblage with diverse invertebrates, vertebrates, fungi, and plants (Mendes *et al.*, 2020). The Crato biota are almost exclusively conserved in the C6 limestone layer (Corecco *et al.*, 2022). Crato fossils commonly appear as an orange to brown friable material or as a seemingly amorphous dark matter (Bezerra *et al.*, 2020; Dias & Carvalho, 2022). The orange to brown specimens are preserved by oxy-hydroxide after pyrite, while the coalified fossils occur as carbonaceous compressions (Bezerra *et al.*, 2021). The strata of the Crato Formation are of uncertain age as estimates vary depending on the method applied (e.g., isotope-analysis, ostracod and palynomorph assemblages, microfossil data) (Arai, 2014; Arai & Assine, 2020; Coimbra *et al.*, 2002; Coimbra & Freire, 2021; Heimhofer & Hochuli, 2010; Lúcio *et al.*, 2020; Melo *et al.*, 2020). However, all methods agreed on an age constraint between the Late Barremian and Early Albian or ca. 122–113 mya (Bezerra & Mendes, 2024).



Sequ.	Group	Formation	Lithology
Post Rift II	Araripe	Exu	Sandstone
		Araripina	Sand., Silt.
Post Rift I	Santana	Romualdo	Concretions
		Ipubi	Gypsum
		Crato	Limestone
		Barbalha	Sand., Shal.
Rift	Vale do Cariri	Abaiara	Sand., Silt.
		Missão Velha	Sandstone
		Brejo Santo	Claystone
		Cariri	Sandstone
		Basement	Granite

FIGURE 1. Simplified geological map of the Araripe Basin. The stratigraphic column is summarized at the right (modified from Assine, 2007).

The Crato fossils have primarily been interpreted as having lived in a lacustrine environment because of the absence of typically marine specimens (Heimhofer *et al.*, 2010; Catto *et al.*, 2016). The presence of halite pseudomorphs in different carbonate levels of the Crato Formation suggests deposition under fluctuating salinity conditions (Martill *et al.*, 2007). Several authors have suggested that these carbonates were deposited in a hypersaline lagoon system with restricted connection to an epeiric sea (Assine *et al.*, 2016). Whether the Crato limestones were deposited in a freshwater lake, or temporarily in a brackish lagoon is still a matter of debate.

Materials and methods

The specimens presented in this study were part of two German collections (the Husemann Research Collection (HRC) managed by author MH and the collection of the Museum der Natur—Paläontologie/Geologie, Hamburg, Germany, managed by author UK). As part of the guidelines discussed at the "Brazil-German Colloquium on Paleontology: Science, Cooperation, and Diplomacy for the Future" They were deposited at the Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil. Specimens MPSC 9841 (ex coll. no. CNBS00410), MPSC 9842 (ex coll. no. CNBS00419), and MPSC 9840 (ex coll. no. CNBS00421) were provided from the latter institution. MPSC 9839 (ex coll. no. HC0008) and MPSC 9838 (ex coll. no. HC0011) were donated from the HRC. The non type specimen CNBS00417 is housed in the Museum der Natur—Paläontologie/Geologie collection.

Imaging of the specimens was done using a Keyence VHX-6000 digital microscope (KEYENCE Corporation, 2024, Osaka, Japan; https://www.keyence.com/). All images are composite images assembled via the stitching method. Drawings of the specimens were created in GIMP (v. 3.0.2-1) (the GIMP Team, 2025; https://www.gimp.

org/). Figures were assembled and modified (scale bars and labelling) in Inkscape (v. 1.4.2) (the Inkscape Team, 2025; https://inkscape.org/).

The taxonomy in this study follows the Orthoptera species file (Cigliano *et al.*, 2025; https://orthoptera.speciesfile.org/). Wing venation nomenclature follows Béthoux & Nel (2002) with abbreviations: CP posterior costa; ScA, ScP = anterior/posterior subcosta; R = radius; RA, RP = anterior/posterior radius; MA, MP = anterior/posterior media; CuA, CuP = anterior/posterior cubitus; CuPaα = anterior branch of first posterior cubitus; CuPaβ = posterior branch of first posterior cubitus; CuPb = second posterior cubitus; 1A = anterior anal vein.

Systematic paleontology

Order Orthoptera Latreille, 1810

Suborder Caelifera Ander, 1936

Family Locustopsidae Handlirsch, 1906

Genus *Aestuacrida* new genus

urn:lsid:zoobank.org:act:A2294EFF-9104-4340-B88A-0059EFD0CCFF

Type species: *Aestuacrida stereofemoris* **sp. nov.** by monotypy and present designation. Gender feminine.

Etymology: The genus name is a combination of the Latin *aestuarium* (lagoon) and the suffix *-acrida*. It refers to the hypothesized habitat of the Crato Formation in which the genus is thought to have lived.

Diagnosis: The new genus is characterized by having two branches of M as well as four branches of CuA + CuPaα in the forewing.

Remarks: The new genus can be attributed to Locustopsidae by its separated RP, M, and CuA + CuPaα, as well as a long ScP and singular RA. Its main diagnostic character—the presence of four branches of CuA + CuPaα—highlights the great diversity of this family in the Crato Formation, as the trait is unique to this genus and locality.

Aestuacrida stereofemoris new species

urn:lsid:zoobank.org:act:F6C61C1D-227D-4533-910E-10D633830634

Fig. 2

Etymology: The species name refers to the heavily built metafemora. It is derived from the Ancient Greek *stereós* (solidly built) and Latin *femur*.

Locality and horizon: Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Early Cretaceous, Aptian.

Type material: Holotype male in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil, coll. no. MPSC 9838.

Diagnosis: Overall stocky body and very sturdy hind femurs (length/width-ratio ca. 3.0). Origin of tegminal RP distinctly posterior to forking of M. RP with five or six branches. Cross vein pattern relatively simple.

Description: The specimen has body, wings, left hindleg and part of the right hindleg preserved.

Measurements: Body length 12.9 mm, height (measure taken at thorax) 4.7 mm. Head height 3.3 mm. Forewing length 16 mm, height 2.8 mm. Metafemur 8.3 mm long, ca. 2.8 mm wide. Metatibia 7.1 mm long. Metatarsus 2.2 mm long.

Body: Body rather stocky (length/height-ratio 2.74). Head rather short, much shorter than thorax.

Legs: Metathoracic femur very sturdy, length/height-ratio 3.0. Oblique lateral carinae present. Metatibia narrow with no apparent spination other than 2 (?) apical spurs. Metatarsus with no spines or lobes.

Forewing: Length/height-ratio 5.7. ScP long and narrow, at least 81.5% of total wing length (twl) (venation not preserved in most distal part of wing; ScP would have been longer). Space between ScP and RA 9.4% of total

wing height (twh). Origin of RP at 54.5% of twl, distinctly posterior to fork of M. Space between RA and RP 11.3% of wing height. RP with 5 or 6 branches (attribution of RP3 to forewing or hindwing unsure due to strong wing overlap; we suggest RP of forewing with 5 branches). M with two branches; fork of M at 44.5% of twl. CuA + CuPaα with four branches; anterior branch reaching anal margin of forewing at ca. 69.8% of twl. Second branch probably reaching anal wing margin too. Third and fourth branch do not reach anal wing margin but make contact with CuPaβ. CuPaβ reaching anal wing margin at ca. 62.6% of twl. Cross vein pattern rather simple; consisting mainly of simple orthogonal cross veins set at rather wider distance.

Remarks: The single species of this genus is characterized by relatively thick hindfemora. Whether this trait is a common feature of *Aestuacrida* remains unanswered until additional species are described. Unfortunately, most locustopsids do not have their hindlegs well-preserved, hence providing little applicability to the character of femur width regarding taxonomy of the family.

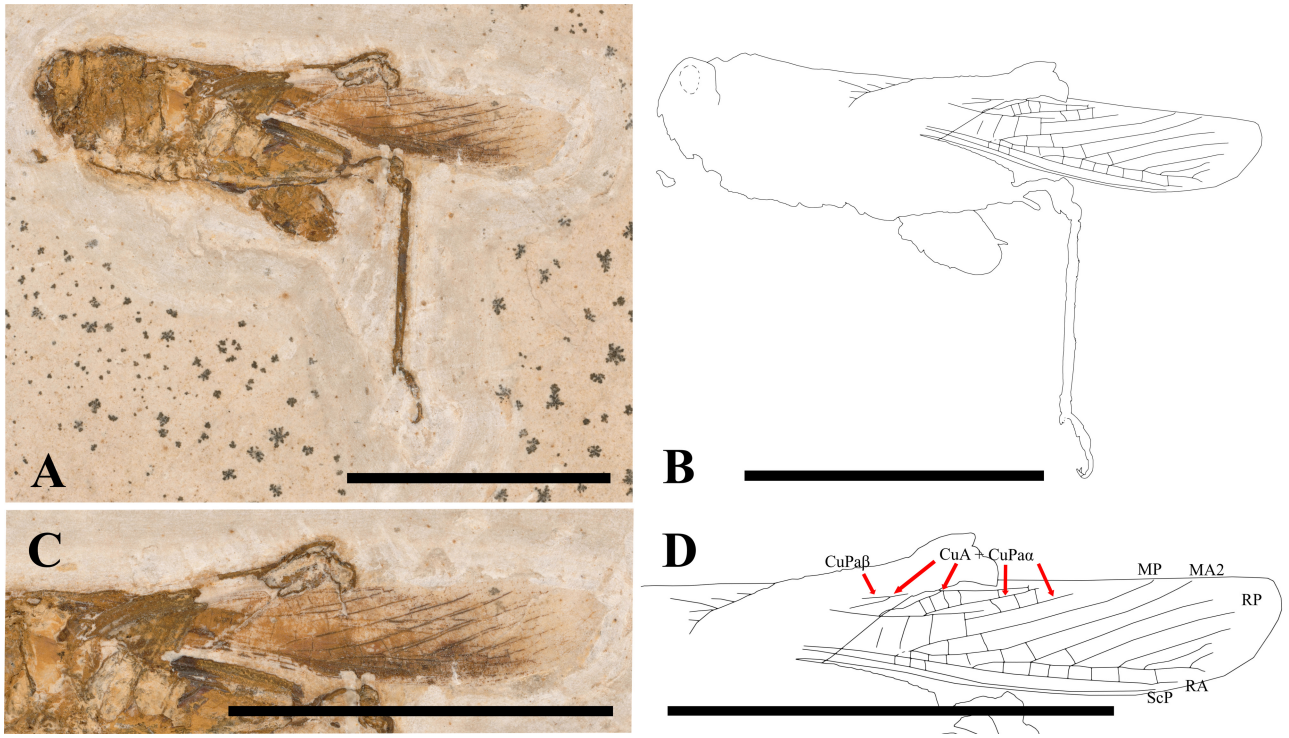


FIGURE 2. *Aestuacrida stereofemoris* **gen. et sp. nov.** holotype male, MPSC 9838. **A.** and **B.** Image and drawing of complete specimen. **C.** and **D.** Image and drawing of the forewing. **Scale bars** = 10 mm.

Genus *Parapleurites* Brauer, Redtenbacher & Ganglbauer, 1889

Included species: *Parapleurites gracilis* Brauer, Redtenbacher & Ganglbauer, 1889 (type species); *P. sibiricus* Sharov, 1968; *P. brasiliensis* **sp. nov.**

Parapleurites brasiliensis new species

urn:lsid:zoobank.org:act:F7CF6ED7-4E39-475D-9F0F-C108651F9BBB
Fig. 3

Etymology: The species is named after its home country Brazil.

Locality and horizon: Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Early Cretaceous, Aptian.

Type material: Holotype male, in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil, coll. no. MPSC 9839.

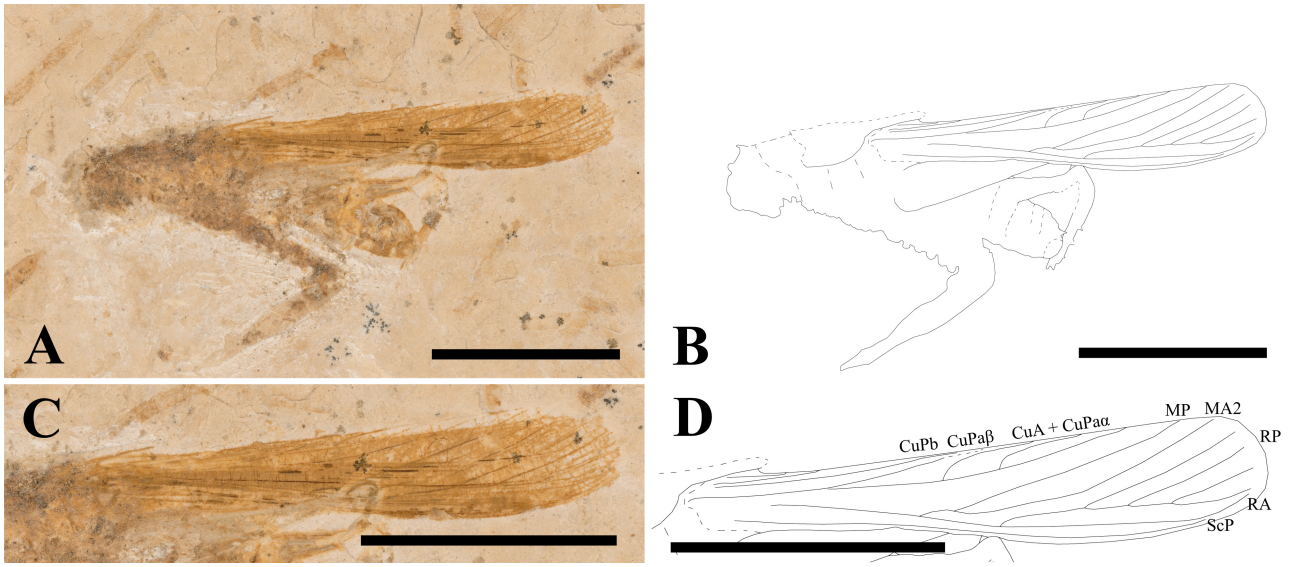


FIGURE 3. *Parapleurites brasiliensis* **sp. nov.** holotype male, MPSC 9839. **A.** and **B.** Image and drawing of complete specimen. **C.** and **D.** Image and drawing of the forewing. **Scale bars** = 10 mm.

Diagnosis: Characterized by having three branches of CuA + CuPaα and two branches of M—a combination that places it within the genus *Parapleurites*. Third and second branches of CuA + CuPaα strongly concave, first branch convex. RP with four branches. Fork of M above between second and third branches of CuA + CuPaα, slightly inclined toward third branch. Origin of RP distinctly posterior to fork of M. Pronotum possibly rather shallow with elongated hind lobe (pronotal shape not clearly discernible).

Description: Specimen with impression of body, forewing, metafemurs and proximal part of the right metatibia preserved.

Measurements: Body length 18 mm. Metafemur ca. 11.2 mm long, 2.4 mm wide. Forewing length 21.6 mm, height 4.05 mm. Pronotum 7.9 mm long (?), 2.1 mm high (pronotum outline unclear).

Body: Body cylindrical, little alteration in height, "sausage-like" shape. Pronotum outline unclear; possibly very elongate and shallow. Abdominal height dominated by tergites (ca. 79%). Ventral side with conspicuous structure of uncertain identity; possibly associated with fossilized plant material present in matrix).

Legs: Only metafemur and proximal portion of metatibia preserved. Metafemur length/height ratio 4.7; oblique lateral carinae present; genicular joint not significantly wider than metatibia. Three small spines discernible on posterior half of metatibia.

Forewing: Length/height ratio 5.3. ScP long, narrow, extending beyond 89.2% of twl. RA distinctly curved upward near distal margin. Distance between ScP and RA 10.9% of twh. RP originates at 53.9% of twl, posterior to fork of M. Distance between RA and RP broad (15.2% of wing height). RP with four branches. M with two branches; fork of M at 46.3% of twl. CuA + CuPaα with three branches, all reaching anal margin at 76.3%, 68.5%, and 60.2% of twl, respectively. Anterior branch convex; second and third strongly concave. CuPaβ reaches anal margin at 51.2% of twl. CuPaβ, CuPb, and 1A narrow and parallel.

Remarks: The new species can be assigned to *Parapleurites* based on the presence of two branches of M and three branches of CuA + CuPaα. It differs from the type species, *P. gracilis*, in several characters: it is significantly larger (forewing length 14 mm in *P. gracilis*) and exhibits a longer ScP (72.7% of total wing length in *P. gracilis*). Additionally, the second branch of CuA + CuPaα is strongly concave in *P. brasiliensis* **sp. nov.**, whereas both the first and second branches are strongly convex in *P. gracilis* (third branch in *P. gracilis* is likely concave). Another distinguishing feature is the position of the RP origin, which is anterior to the fork of M in *P. gracilis*, but posterior in *P. brasiliensis*. The stratigraphic and geographic provenance further differentiates the species: *P. gracilis* originates from the Lower Jurassic of Siberia, while *P. brasiliensis* is from the Lower Cretaceous of Brazil. From *P. sibiricus*, the new species differs by having one fewer branch of RP as well as the position of RP origin, which is proximal to the fork of M in *P. brasiliensis*. *Parapleurites sibiricus* is known from the Middle Jurassic of Siberia. *Parapleurites*

morrisonensis Smith, Gorman, Pardo & Small, 2011 from the Upper Jurassic Morrison Formation of North America, does not have three branches of CuA + CuPaα and should not be retained in *Parapleurites*. Its venation features—three branches of M and single branch of CuA + CuPaα, with MP and CuA + CuPaα fused in the holotype—suggests a more appropriate placement in *Mesolocustopsis*.

Genus *Cratolocustopsis* Martins-Neto, 2003

Included species: *Cratolocustopsis cretacea* (Martins-Neto, 1990) (type species); *C. contumax* Martins-Neto, 2003; *C. aquila* **sp. nov.**

Remarks: *Cratolocustopsis* was originally described by Martins-Neto (2003) as having forewing with two branches of CuA + CuPaα (referred to as MP + CuA in the original text) and a relatively short and robust hindfemur, with a width/length ratio ranging from 0.2 to 0.35. Unfortunately, the drawings given in the same publication for species assigned to *Cratolocustopsis* did not match this description, leading to taxonomic uncertainty regarding the validity of the genus (e.g., Gorochov *et al.*, 2006). In addition to the new species of *Cratolocustopsis* described herein, we report a new specimen that, based on its morphology and original description of *Cratolocustopsis cretacea* (Martins-Neto, 1990), can be confidently assigned to that species. This new specimen reveals the presence of two branches of CuA + CuPaα—features that were not depicted in the original figure provided by Martins-Neto—thus reaffirming the diagnostic traits of the genus.

Cratolocustopsis aquila sp. nov.

urn:lsid:zoobank.org:act:6013C196-AEE9-4A17-9992-196C40D28AAB
Fig. 4

Etymology: The species name derives from the Latin *aquila*, meaning "eagle". It refers to the head shape of the specimen, which resembles the beak of a bird of prey. This appearance is the result of damage to the fossil and does represent the actual morphology of the species.

Locality and horizon: Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Early Cretaceous, Aptian.

Type material: Holotype, sex unknown, in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil, coll. no. MPSC 9840.

Diagnosis: Species recognized by MP strongly concave in distal fourth, almost parallel to anal wing margin. RP originates posterior to fork of M. RP bifurcates shortly after origin. Note: latter character may represent an individual aberration.

Description: Body, forewing and left metafemur as well as most of metatibia preserved.

Measurements: Body length 20.4 mm; abdomen ca. 10.3 mm. Head height 4.3 mm. Metafemur 12.1 mm long, 2.6 mm wide. Preserved part of metatibia 8.8 mm long. Forewing length 24.6 mm, 4.1 mm high.

Legs: Length/height-ratio of metafemur 4.65. Oblique lateral carinae present. Metatibia with 7 small dorsal spines on preserved part (probably ca. 80% of metatibia length preserved).

Forewing: Length/height-ratio 6. ScP length at least 85.9% of twl. Space between ScP and RA 11.4% of total wing height. Origin of RP at 50.5% of twl, posterior to M bifurcation. Space between RA and RP rather wide, 15% of wing height. RP with four branches. Shortly after its origin, RP is bifurcated; the upper branch is the "normal" RP, considered as RP1. Lower branch is fused to RA slightly anterior to branching of RP4. M with two branches. Fork of M at 45.9% of twl. Anterior and posterior branch of M parallel along most of their length, however MP describing a strong concave curve distally, almost making contact with MA2 as the latter touches wing margin. CuA + CuPaα with two branches. Anterior branch relatively parallel to MA2, reaching wing margin at 72.7% of twl. Posterior branch strongly concave similar to distal part of MP. Base of CuA + CuPaα (connection to CuPaβ) at 30% of twl. CuPaβ reaching anal wing margin at ca. 42.5% of twl (anal wing margin slightly damaged in the fossil, last millimeters of branch are lost). Cross vein pattern rather simple, consisting mainly of straight cross veins.

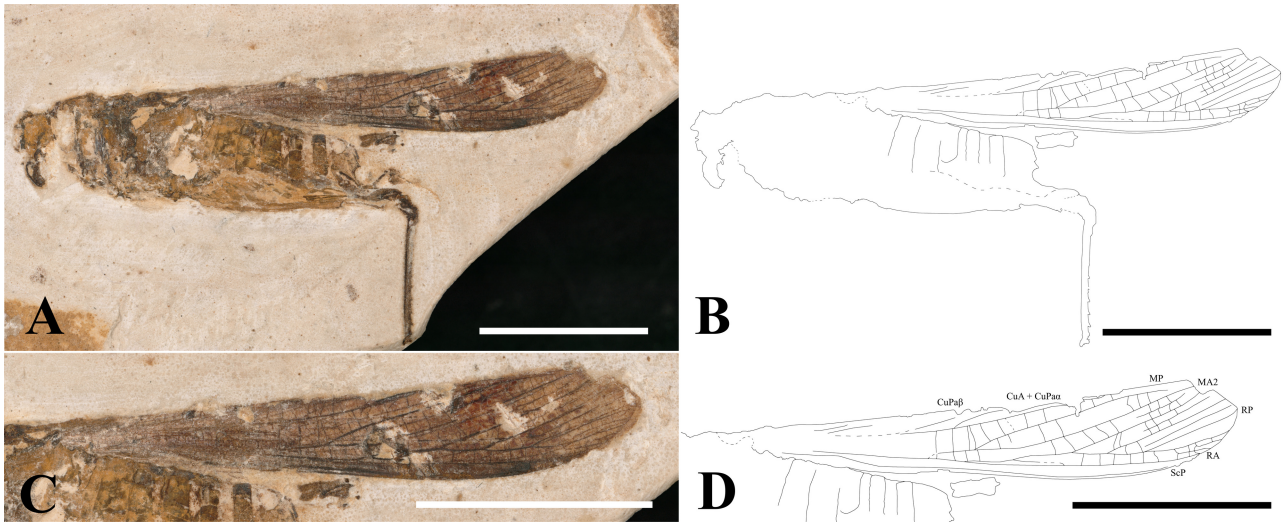


FIGURE 4. *Cratolocustopsis aquila* **sp. nov.** holotype, sex unknown, MPSC 9840. **A.** and **B.** Image and drawing of complete specimen. **C.** and **D.** Image and drawing of the forewing. **Scale bars** = 10 mm.

Remarks: Cratolocustopsis aquila **sp. nov.** is assigned to *Cratolocustopsis* based on the presence of two branches of CuA+ CuPaα and two branches of M. It differs from *C. cretacea* by its MP being strongly concave distally (MP is parallel to MA2 along its entire length in *C. cretacea* (Fig. 6A in Martins-Neto (2003) and Fig. 5 from this study). *Cratolocustopsis aquila* further differs from the type species by the distal extent of the CuA + CuPaα branches: in the new species, both branches reach the wing margin, whereas in *C. cretacea*, only the anterior branch does so, with the posterior branch terminating in contact with CuPaβ. The new species also differs from *C. contumax* by being significantly larger; the forewing of *C. contumax* measures 18 mm in length, whereas that of *C. aquila* is 24.6 mm long.

***Cratolocustopsis cretacea* (Martins-Neto, 1990)**
Figs. 5, 6

Locality and horizon: Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Early Cretaceous, Aptian.

Type material: Holotype male (coll. no. GP/1T-1671) and paratype male (coll. no. GP/1T-1618a), both specimens are in the collection of Instituto de Geociências da Universidade de São Paulo (IGc/USP) (Fig. 6).

Additional material examined in this study: A relatively well-preserved specimen of uncertain sex in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil, coll. no. MPSC 9841. Donation from Museum der Natur—Paläontologie/Geologie (Museum of Nature—Palaeontology/Geology), Hamburg, Germany (Collection number CNBS_00410), as part of the guidelines discussed at the "Brazil-German Colloquium on Paleontology: Science, Cooperation, and Diplomacy for the Future".

Description of new material: Large parts of the body and wings preserved. Missing are most details of the prothoracic leg, the mesothoracic leg as well as the tarsus of the metathoracic leg. Structures of the abdominal apex obscured by metathoracic legs.

Measurements: Body length (head to abdominal apex) 17.9 mm. Head height 3.6 mm. Pronotum length 8.65 mm. Metafemur ca. 11.4 mm long. Metatibia (as preserved) 9.9 mm long. Forewing 20.6 mm long, 3.4 mm high.

Body: Head relatively small. Pronotum rather large and posteriorly elongated. Lateral margin with very prominent concave curve.

Legs: Prothoracic leg inconspicuous. Femur slightly wider than tibia. Metathoracic leg: femur relatively slender. Distal half of tibia dorsally with some small spines of which four are preserved.

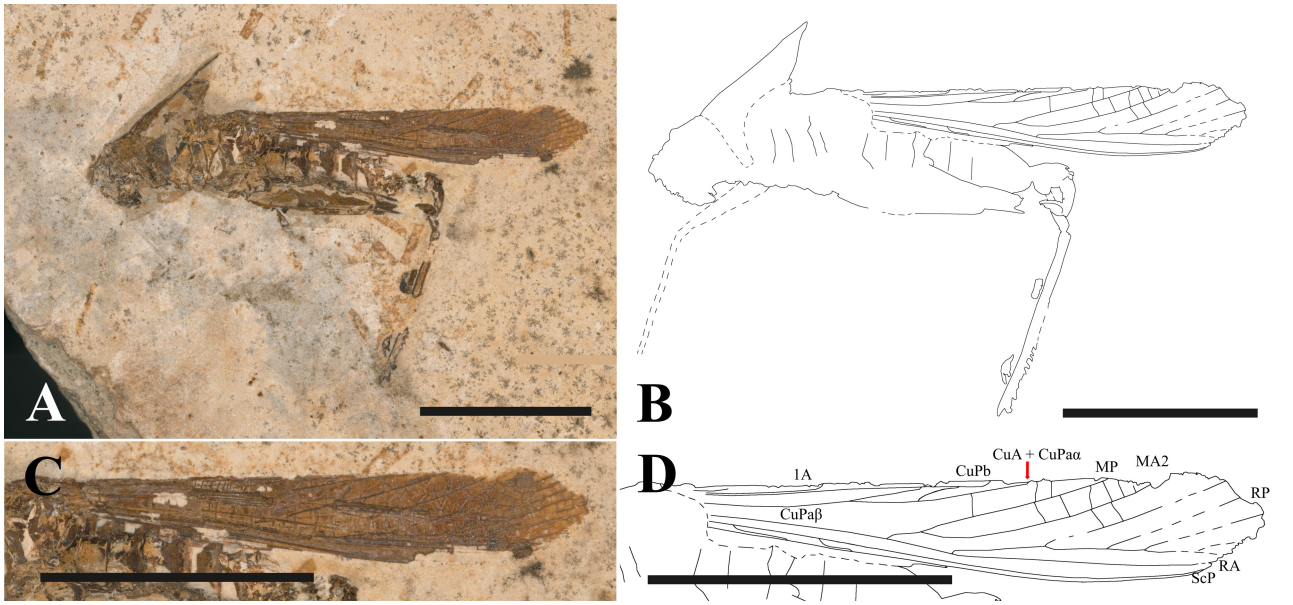


FIGURE 5. *Cratolocustopsis cretacea* (Martins-Neto, 1990), specimen MPSC 9841 (not a type). **A.** and **B.** Image and drawing of complete specimen. **C.** and **D.** Image and drawing of the forewing. **Scale bars** = 10 mm.

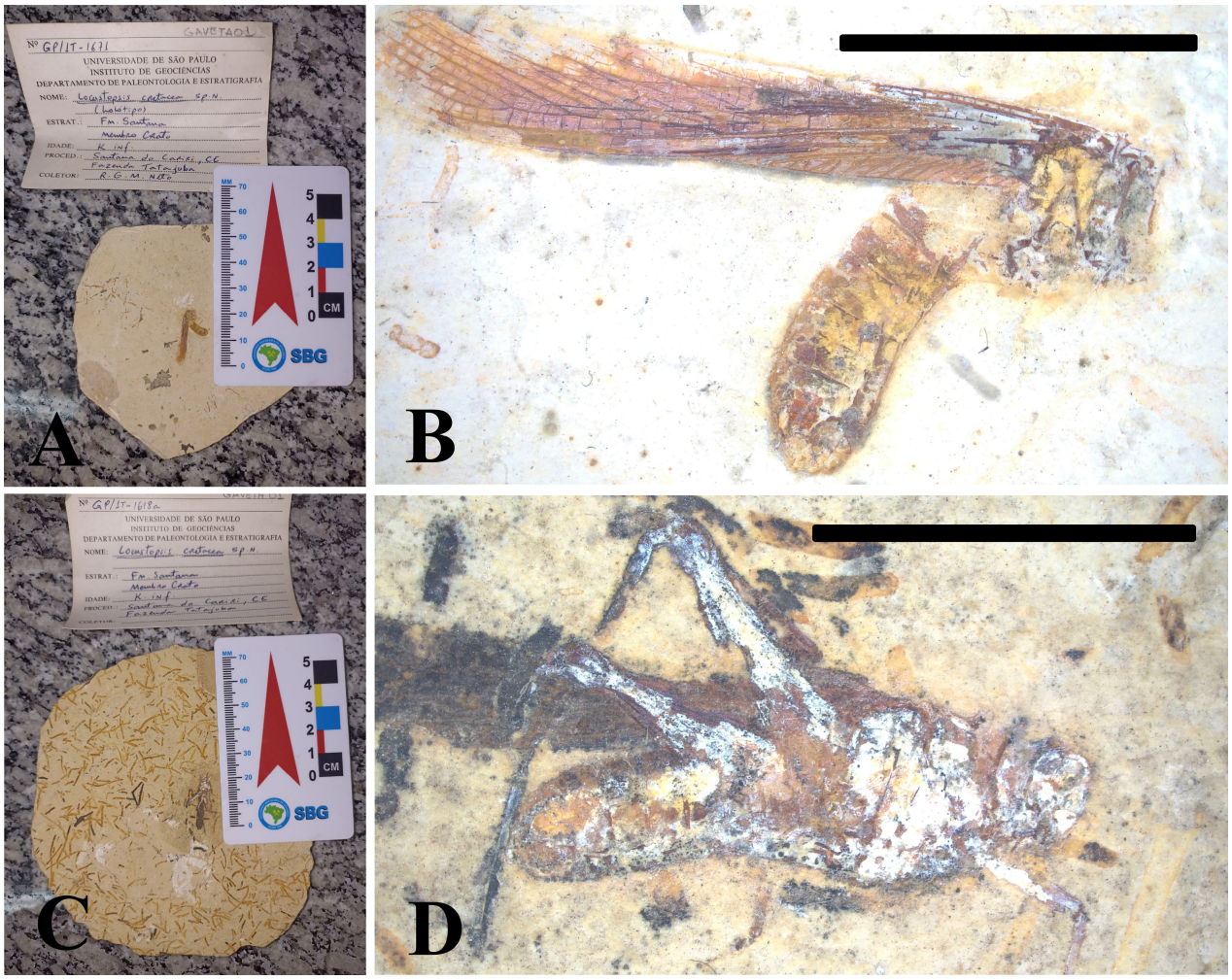


FIGURE 6. Holotype (GP/1T-1671) and paratype (GP/1T-1618a) in the collection of Instituto de Geociências da Universidade de São Paulo (IGc/USP) of *Cratolocustopsis cretacea* (Martins-Neto, 1990). **A.** and **B.** Holotype. **A.** shows a museum label proving the identity of the holotype. **C.** and **D.** Paratype. **C.** shows a museum label proving the identity of the paratype. Image credits to Marcela F. Colombo.

Forewing: Length/height-ratio 6.1. ScP length at least 89% of twl. Termination of ScP (costal wing margin or fused to RA) not preserved. Space between ScP and RA 13.6% of total wing height (measured between RP4 and RP5). Origin of RP at 48.1% of twl, posterior to M bifurcation. Space between RA and RP 14% of wing height. RP with five branches. M with two branches. Fork of M at 43% of twl. Branches of M and RP more or less parallel. CuA + CuPaα with two branches. Anterior branch relatively parallel to M and RP, reaching wing margin at 61.3% of twl. Posterior branch strongly concave and fused to CuPaβ. Base of CuA + CuPaα (connection to CuPaβ) at 31.5% of twl. CuPaβ not reaching anal wing margin but fused to CuPb at 43.3% of twl. CuPb long and narrow, reaching anal wing margin after 54.8% of twl. 1A narrow, reaching anal wing margin after 27% of twl. Cross vein pattern unsure due to overlapping of fore- and hindwings.

Remarks: The specimen MPSC 9841 originates from the same stratigraphic unit (Crato Formation) and general geographic region as the holotype of *Cratolocustopsis cretacea*. It preserves diagnostic features consistent with the original description and emended diagnosis of *C. cretacea*, including a forewing with two branches of CuA + CuPaα and two branches of M. The description of the additional specimen will hopefully provide reference for future comparative and systematic studies.

Subfamily Araripelocustinae Martins-Neto, 1995

Genus *Araripelocusta* Martins-Neto, 1995

Included species: *Araripelocusta longinota* Martins-Neto, 1995 (type species); *A. brevis* Martins-Neto, 1995; *A. imperatrix* **sp. nov.**

Araripelocusta imperatrix new species

urn:lsid:zoobank.org:act:2C21DFDC-A19A-458A-86E8-A3EB48B4D793
Figs. 7–9

Etymology: The species name is derived from the Latin word *imperatrix*, meaning "female sovereign". It refers to the rather large size of the specimen, which makes it the largest known species of its genus. The name also alludes to the leaf-like appendages on the head, which resembles a crown or antlers.

Locality and horizon: Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Early Cretaceous, Aptian.

Type material: Holotype female, in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil, MPSC 9842. Paratype female, in the collection of Museum der Natur—Paläontologie/Geologie, Hamburg Germany, coll. no. CNBS00417.

Diagnosis of species: Large species; forewing length 37.8–39.1 mm. Hindwing with conspicuous dark band near distal margin and irregular dark blotches across wing surface. Wings very elongate with length/width-ratio of forewing 7.4. RP with five branches. Apex of head bearing two leaf-like appendages with fine lateral spines/hairs (Fig. 9). Ovipositor straight, 5.5 mm long.

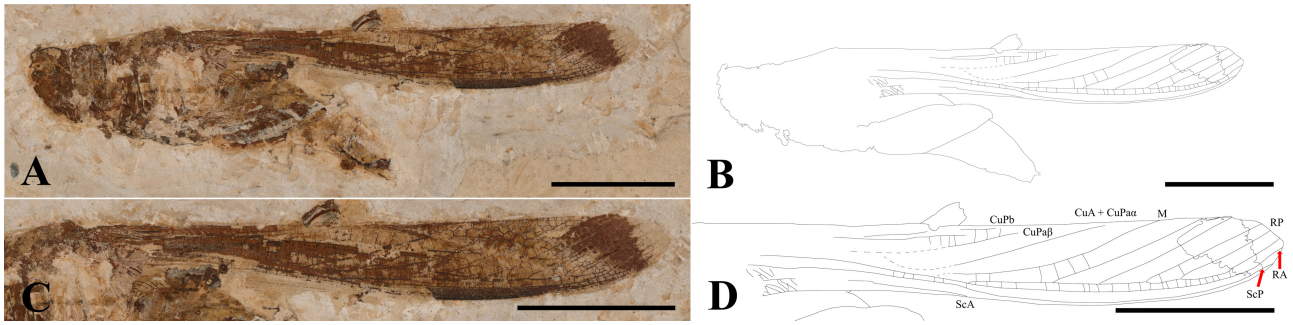


FIGURE 7. *Araripelocusta imperatrix* **sp. nov.** holotype female, MPSC 9842. **A.** and **B.** Image and drawing of complete specimen. **C.** and **D.** Image and drawing of the forewing. **Scale bars** = 10 mm.

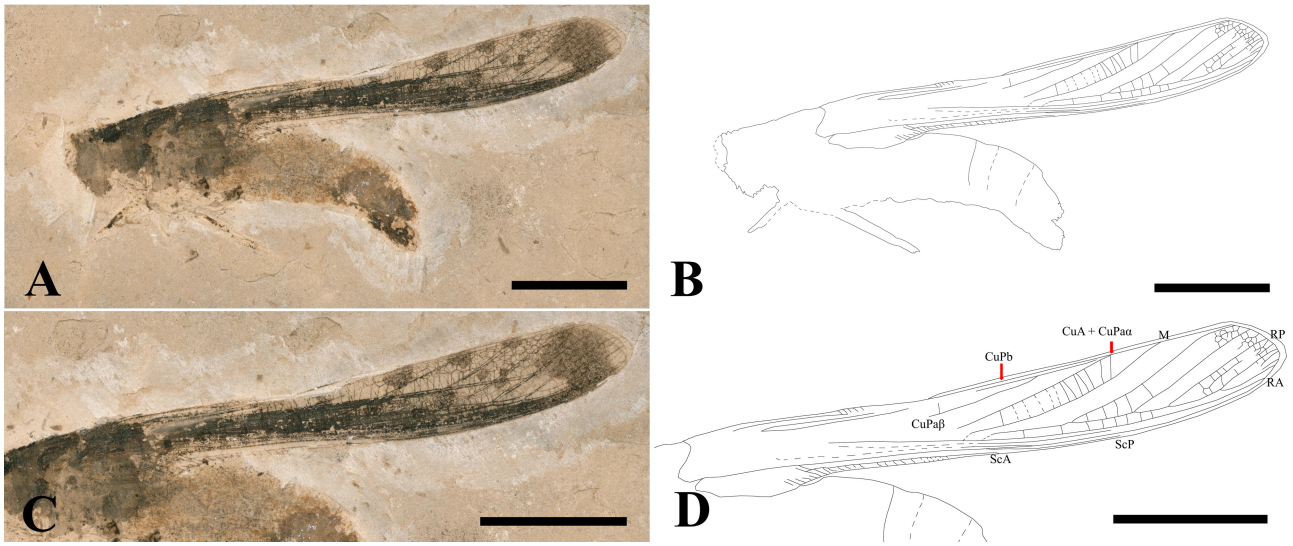


FIGURE 8. *Araripelocusta imperatrix* **sp. nov.** paratype CNBS_00417. **A.** and **B.** Image and drawing of complete specimen. **C.** and **D.** Image and drawing of the forewing. **Scale bars** = 10 mm.

Description of holotype: Head, body, wings and fragmented metathoracic leg.

Measurements: Body length 30.1 mm. Head height 6.2 mm. Appendages of head 0.85 mm. Ovipositor 2.1 mm (fragmented). Forewing length 37 mm, 5 mm high.

Body: Head conically pointed with front convexly curved. On the top of the head above the eyes is a pair of leaf-shaped appendages somewhat like little antlers. Anterolateral margin of appendages distally with fine spines or hairs. Pronotum saddle-shaped, exact outline unsure. Valvulae of ovipositor broad.

Legs: Attribution of fragmentary metathoracic leg parts unsure; either rather broad metafemur or metatibial folded in front of metafemur. Apparently with oblique lateral carinae on metafemur.

Forewing: Length/height-ratio 7.4. ScA narrow with multiple branches, reaching anterior wing margin at 41% of twl. ScP length 97.8% of wing length, slightly turned upwards distally. Space between RA and ScP 13.3% of total wing height. Origin of RP at 41.5% of twl, relatively close to M veering off RA. Space between RA and RP 10.7% of total wing height. RA distinctly turned upwards distally. RP with five branches; RP1 distinctly turned upwards parallel to RA. M with one branch, parallel to RP branches. CuA + CuPaα with one branch, reaching anal wing margin at ca. 67.6% of twl (contact point not discernible). CuPaβ parallel to CuA + CuPaα. Base of CuA + CuPaα at 25.8% of twl. Cross vein pattern rather simple over majority of wing surface but getting very complicated and net-like towards distal area between M and RP as well as branches of RP.

Description of paratype: Body outline with fragmented pro- and mesothoracic leg as well as ovipositor preserved. Wing apparatus fully intact.

Measurements: Body length 31.6 mm. Head height 5.9 mm. Eye height 2.0 mm. Ovipositor 5.5 mm. Forewing length 39.1 mm, 5.3 mm high.

Body: Head conically pointed. Valvulae of ovipositor rather prominent (for Caelifera), possibly serrated distally (impression of serration could be due to state of preservation).

Legs: Pro- and mesothoracic extremities slim, almost looking fragile compared to the animal's larger size.

Forewing: Length/height-ratio 7.4. ScA narrow with multiple branches (18+), reaching anterior wing margin at 52% of twl. ScP length at least 72.5% of twl, but likely significantly longer (the branch is lost in the dark coloration present towards the anterior wing margin). Origin of RP at 49.6% of twl, relatively close to M veering of RA. Space between RA and RP 10.5% of total wing height. RP with five branches. M with one branch, parallel to RP branches. CuA + CuPaα with one branch, reaching anal wing margin at 73.1% of twl. CuPaβ parallel to CuA + CuPaα; not reaching wing margin but in contact with CuPb at 60.7% of twl. CuPb very long and narrow, reaching wing margin very shortly anterior of CuA + CuPaα reaching wing margin. Cross vein pattern rather simple over majority of wing surface but getting very complicated and net-like towards distal area between M and RP as well as branches of RP.

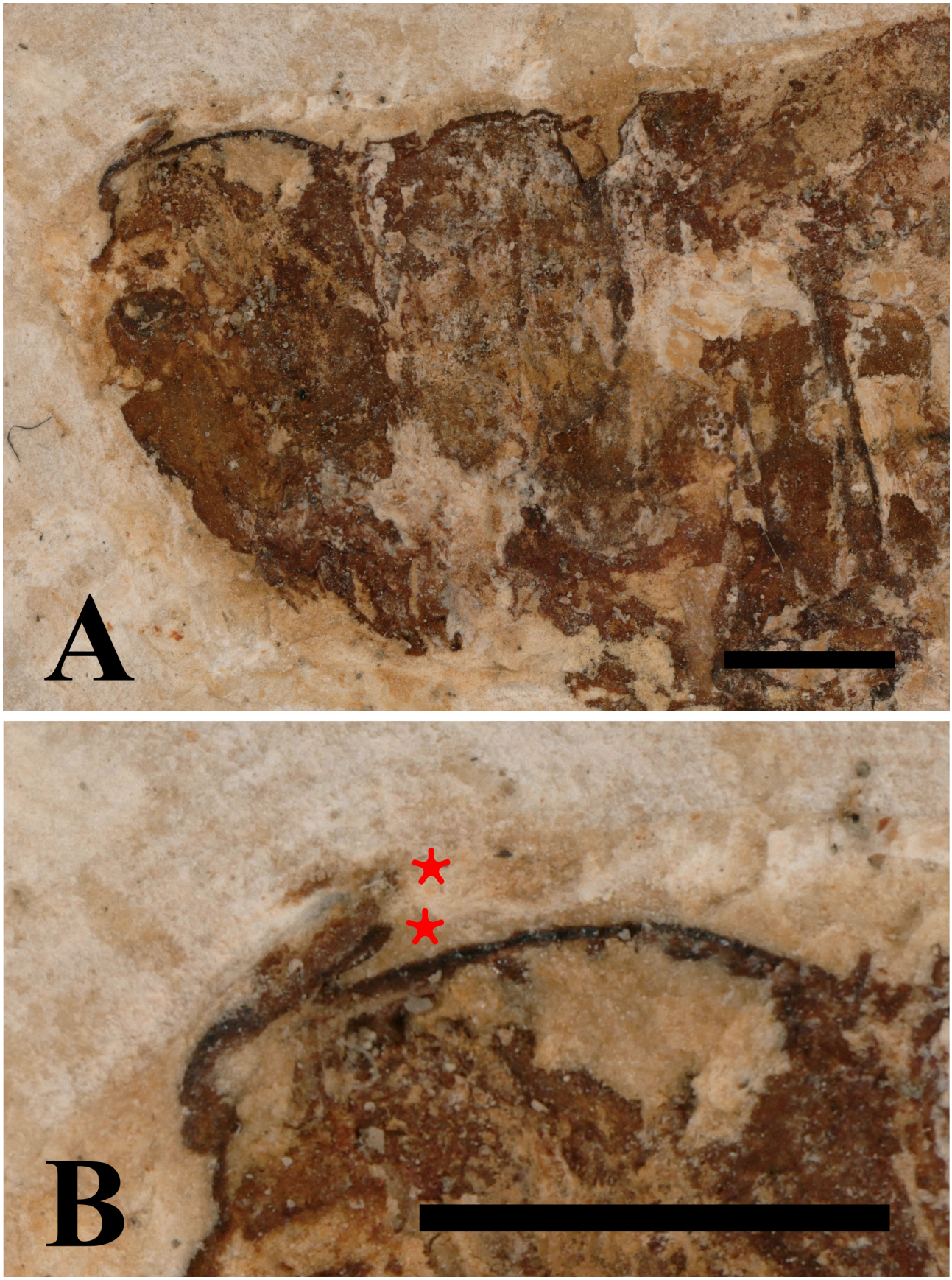


FIGURE 9. *Araripelocusta imperatrix* **sp. nov.** holotype female, coll. no. MPSC 9842. **A.** Detail of head with appendages. **B.** Close-up of antler-like appendages (red stars). **Scale bars** = 2 mm.

Remarks: The new species is assigned to Araripelocustinae based on the presence of a single branch of M, and to *Araripelocusta* due to the presence of a single branch of CuA + CuPaα. *Araripelocusta imperatrix* **sp. nov.** is clearly distinct from the other two species of the genus known from the Crato Formation by being significantly larger, exceeding 37 mm (*A. longinota* and *A. brevis* have forewings about 22.5 mm long (Martins-Neto & Gallego, 2006)). It further differs from its congeners as well as all known species of Locustopsidae so far by having a pair of small, leaf-like appendages located dorsally above the eyes, reminiscent of antlers. The precise identity of this structure remains uncertain; however, the presence of similar shape in the same position in the paratype specimen (Fig. 8), albeit less clearly preserved, supports the interpretation that this appendage is part of its morphology rather than an extrinsic element of the matrix.

Taxonomic revision of Locustopsidae

The taxonomy of Locustopsidae is predominantly based on forewing venation, particularly the number of branches of CuA + CuPaα and M, and the relative position of MA2 in relation to either MP or MA1 when three M branches are present (Tab. 2) (Gorochov *et al.*, 2006). Previous revisions of Gorochov *et al.* (2006) and Gorochov & Coram (2023) proposed several significant changes to the internal classification of the family. These include the tentative synonymy of *Cratozeunerella* Martins-Neto, 1998 with *Zeunerella* Sharov, 1968, and *Cratolocustopsis* Martins-Neto, 2003 with *Mesolocustopsis* Hong & Wang, 1990 (Gorochov & Coram, 2023). The inclusion of *Locustopsis anatolica* Sharov, 1968 in *Schwinzia* Zessin, 1983 was also suggested (Gorochov & Coram, 2023). Furthermore, *Zessinia caririensis* Martins-Neto, 1990, *Z. petruleviciusi* Martins-Neto, 2003, and *Z. vikingi* Martins-Neto, 2003 were proposed to be transferred to *Mesolocustopsis* (Gorochov *et al.*, 2006). Gorochov & Coram (2023) also pointed out the marginal difference between *Locustopsis* Handlirsch, 1906 and *Plesioschwinzia* Zessin, 1988 (number of branches of ScP) and questioned whether it would suffice to generic separation.

Building upon these prior assessments and incorporating newly examined specimens, we propose the following taxonomic revisions to Locustopsidae:

1. Synonymy of *Cratozeunerella* with *Zeunerella*

The characters originally used (Martins-Neto, 2003) to distinguish *Cratozeunerella*—presence of cross veins in subcostal area, one to two additional RP branches in fore- and hindwings—are insufficient for generic separation and better reflect species-level differences. We agree with Gorochov & Coram (2023) that *Cratozeunerella* should be synonyized with *Zeunerella*. However, four species formerly attributed to *Cratozeunerella—C. godoii* Martins-Neto, 2003, *C. nervosa* Martins-Neto, 2003, *C. soaresi* Martins-Neto, 2003, and *C. titanella* Martins-Neto, 2003—exhibit MA2 in contact with MA1 (rather than MP), a venational pattern diagnostic of *Locustopsis*, and are thus should be transferred to that genus. *Cratozeunerella amedegnatoi* Martins-Neto, 1998 and *C. neotropica* Martins-Neto, 1998 are proposed to be moved to *Zeunerella*.

2. Transfer of *Locustopsis anatolica* to *Schwinzia*

Locustopsis anatolica displays three branches of both CuA + CuPaα and M, a combination considered apomorphic for *Schwinzia* (Zessin, 1983). We therefore support the transfer of this species to *Schwinzia anatolica* (Sharov, 1968) **comb. nov.**, as proposed by Gorochov & Coram (2023).

3. Transfer and synonymy within *Mesolocustopsis*

Mesolocustopsis is characterized by a single branch of CuA + CuPaα and three branches of M, with MA2 in direct contact to MA1. The species *Zessinia caririensis*, *Z. petruleviciusi*, and *Z. vikingi* match this venation pattern (see Martins-Neto, 2003; figs. 3A & 5A, 5D & 5F, 4A & 4C), and are thus retained within *Mesolocustopsis*. We further

propose *M. petruleviciusi* as a junior synonym of *M. caririensis*, as the only difference between them—the origin of RP slightly anterior vs. posterior to the fork—is likely due to intraspecific variation.

4. Synonymy of *Plesioschwinzia* with *Locustopsis*

We agree with Gorochov & Coram (2023) that the variation in the number of ScP branches (1–4 in *Plesioschwinzia*; 6–8 in *Locustopsis*) does not warrant generic distinction. This variation is likely due to intraspecific or interspecific differences rather than deeper phylogenetic divergence. We therefore propose *Plesioschwinzia* as a junior synonym of *Locustopsis*.

5. *Cratolocustopsis* and *Mesolocustopsis* are not synonyms

While *Mesolocustopsis* is defined by one branch of CuA + CuPaα and three branches of M (with MA2 contacting MA1), *Cratolocustopsis* possesses two branches of both CuA + CuPaα and M. These character combinations justify their distinction as separate genera. Unfortunately, earlier figures of *C. cretacea* and *C. contumax* (Martins-Neto, 2003) did not clearly depict these venation patterns. However, review of the holotype as well as new material of *C. cretacea* confirms the diagnostic features of *Cratolocustopsis* and supports its validity.

6. Synonymy of German *Locustopsis* species

A detailed re-evaluation of *Locustopsis* species from the Lower Jurassic of Germany (Handlirsch, 1906, 1939; Zessin, 1983) revels substantial morphological overlap:

- *Locustopsis elongata* Handlirsch, 1906 is morphologically indistinguishable from *L. elegans* Handlirsch, 1906 and is herein considered a junior synonym of the latter.
- *Locustopsis lacera* (originally *Plesioschwinzia lacera* Zessin, 1983) is highly similar to *L. gyra* Zessin, 1983 from the same region and era (Lower Jurassic of Germany) and is proposed as junior synonym of *L. gyra*.

7. Transfer of *Zeunerella reticulata* to *Cratolocustopsis*

Zeunerella reticulata (Handlirsch, 1939) has two branches of both CuA + CuPaα and M (Zessin, 1983, Fig. 21), consistent with the diagnosis of *Cratolocustopsis*. Although a distal bifurcation of MP may indicate a relic third M branch, the overall venation pattern supports the transfer of this species to *Cratolocustopsis reticulata* (Handlirsch, 1939) **comb. nov.**

8. Taxonomic status of *Sinolocustopsis* Nel & Huang, 2024

Sinolocustopsis elongatus was recently described from the Middle Jurassic of Yan'an Formation, China based on a well-preserved forewing by Nel and Huang (2024). Its venation—particularly the three M branches and two CuA + CuPaα branches—closely matches *Locustopsis*, and we propose its transfer to *Locustopsis* as *L. elongatus* (Nel & Huang, 2024) **comb. nov.** (not to be confused with *L. elongata* (Handlirsch, 1906), considered a junior synonym of *L. elegans* Handlirsch, 1906; see above).

The second species, *Sinolocustopsis brevis* Nel & Huang, 2024, is based on an almost complete forewing with only the basal part missing and two partly preserved paratypes. The holotype shows M as in *Locustopsis* but has only a single branch of CuA + CuPaα. Therefore, it should probably be included in *Mesolocustopsis* as *M. brevis* **comb. nov.** (Nel & Huang, 2024). The two paratypes of *S. brevis* are insufficiently preserved for precise placement. The paratype NIGP206135 (Fig. 2B in Nel & Huang, 2024) may belong to *M. brevis* or *Pseudoacrida* Lin, 1982, depending on the trajectory of CuA + CuPaα. The second paratype NIGP206073 (Fig. 2C in Nel & Huang, 2024),

with probably only two M branches and uncertain CuA + CuPaα branches, may represent *Cratolocustopsis* or a new genus, though this cannot be confirmed due to the poor preservation.

9. Additional notes on genera of uncertain status

In addition to the taxonomic changes proposed above, two genera currently assigned to Locustopsidae are problematic and require re-evaluation. *Liadolocusta* Handlirsch, 1906 (single species *L. auscultans* Handlirsch, 1906) from the Lower Jurassic of England and *Locustopsites* Théobald, 1937 (single species *L. gigantea* Théobald, 1937) from the Oligocene of France. *Liadolocusta* was described by Handlirsch (1906) based on a single foreleg with a well preserved tympanal opening. This material lacks sufficient diagnostic material and should be considered a *nomen nudum*.

Locustopsites gigantea is based on an almost completely preserved forewing. The figure given in Théobald (1937) does not match Locustopsidae and more closely resembles Tettigoniidae Krauss, 1902 (as suggested by Gorochov, 1995) and confirmed via pers. comm. from Dr. Olivier Béthoux (MNHN). We therefore propose *Locustopsites* be removed from Locustopsidae and transferred to Tettigoniidae.

Below is a full list of the genera and species of Locustopsidae with the changes to taxonomy proposed above applied:

TABLE 3. Genera and species of Locustopsidae with taxonomic changes from this study. Species and genera affected by any change to taxonomy are marked by an *. *Locustopsites gigantea* Théobald, 1937 is likely a Tettigoniidae and not featured in this list.

Genus (Author)	Species (Author)
Araripelocusta Martins-Neto, 1995	
	longinota Martins-Neto, 1995
	brevis Martins-Neto, 1995
	*imperatrix** **sp. nov.**
Britannacrida Gorochov, Jarzembowski & Coram, 2006	
	distincta Gorochov, Jarzembowski & Coram, 2006
Liadolocusta Handlirsch, 1906	
	auscultans Handlirsch, 1906
Conocephalella Strand, 1926	
	capito (Deichmüller, 1886)
Cratolocustopsis Martins-Neto, 2003	
	*aquila** **sp. nov.**
	contumax Martins-Neto, 2003
	cretacea (Martins-Neto, 1990)
	*reticulata** **comb. nov.** (Handlirsch, 1939)
Locustopsis (= *Plesioschwinzia** **syn. nov.**) Handlirsch, 1906	
	africanus Ansorge, 1991
	apicalis Zherikhin, 1985
	*bernstorffi** **comb. nov.** (Geinitz, 1880)
	brodiei Cockerell, 1916
	bucklandi (Brodie, 1845)
	cockerelli (Handlirsch, 1939)
	constricta Zeuner, 1942
	cubitalis Zeuner, 1942
	dubia Handlirsch, 1939

.....continued on the next page

TABLE 3. (Continued)

Genus (Author)	Species (Author)
	elegans (= *elongata** **syn. nov.**) Handlirsch, 1906
	*elongatus** **comb. nov.** (Nel & Huang, 2024)
	ferghanensis Martynov, 1937
	germari (Münster, 1842)
	*godoii** **comb. nov.** (Martins-Neto, 2003)
	*gracilis** **comb. nov.** Zeuner, 1942
	gyra (= *lacera** **syn. nov.**) Zessin, 1983
	karatavica Sharov, 1968
	*kruegeri** **comb. nov.** Zessin, 1983
	*lacoei** **comb. nov.** Cockerell, 1916
	maculosa Bode, 1953
	nana Handlirsch, 1939
	*nervosa** **comb. nov.** (Martins-Neto, 2003)
	picta Zherikhin, 1985
	posterior Gorochov, Jarzembowski & Coram, 2006
	*procera** **comb. nov.** Zessin, 1983
	pulchella Zessin, 1983
	reducta Handlirsch, 1939
	rhytofemoralis Gu, Yue, Shi, Tian & Ren, 2016
	*sharovi** **comb. nov.** (Gorochov & Coram, 2023)
	shurabica Sharov, 1968
	sippeli Zessin, 1983
	*soaresi** **comb. nov.** (Martins-Neto, 2003)
	spectabilis Zeuner, 1942
	*thalassophila** **comb. nov.** (Zessin, 1988)
	*titanella** **comb. nov.** (Martins-Neto, 2003)
	*uvarovi** **comb. nov.** Zeuner, 1942
Mesolocustopsis Hong & Wang, 1990	
	anglica Gorochov, Jarzembowksi & Coram, 2006
	angusta Gorochov *et al.*, 2006
	araripensis (Martins-Neto, 1990)
	*brevis** **comb. nov.** (Nel & Huang, 2024)
	caririensis (= *petruleviciusi** **syn. nov.**) (Martins-Neto, 1990)
	morrisonensis **comb. nov.** (Smith, Gorman, Pardo & Small, 2011)
	problematica Gorochov *et al.*, 2006
	sinica Hong & Wang, 1990
	vikingi (Martins-Neto, 2003)
*Aestuacrida** gen. nov.	
	*stereofemoris** **sp. nov.**
Orichalcum Whalley, 1985	
	ornatum Whalley, 1985
Parapleurites Brauer, Redtenbacher & Ganglbauer, 1889	

.....continued on the next page

TABLE 3. (Continued)

Genus (Author)	Species (Author)
	gracilis Brauer *et al.*, 1889
	sibiricus Sharov, 1968
	*brasiliensis** **sp. nov.**
Schwinzia Zessin, 1983	
	*anatolica** **comb. nov.** (Sharov, 1968)
	sola Zessin, 1983
Zessinia Martins-Neto, 1990	
	borealis Gorochov *et al.*, 2006
	pulcherrima Martins-Neto, 1990
	reticulata Martins-Neto, 1990
Zeunerella Sharov, 1968	
	*amedegnatoi** **comb. nov.** (Martins-Neto, 1998)
	arborea Sharov, 1968
	mecklenburgica (Zessin, 1983)
	*neotropica** **comb. nov.** (Martins-Neto, 1998)
	prior Gorochov *et al.*, 2006
Locustrix Martins-Neto, 2003	
	audax Martins-Neto, 2003
	gallegoi Martins-Neto, 2003
Pseudoacrida Lin, 1982	
	costata Lin, 1982
	sennlaubi Nel & Jouault, 2022

Conclusions

This study significantly expands the known diversity of Locustopsidae from the Early Cretaceous Crato Formation, Brazil, through the description of one new genus and four new species. These taxa contribute to a better understanding of the morphological variability and evolutionary differentiation within the family, particularly in terms of forewing venation patterns—currently the primary diagnostic basis for genus-level taxonomy in Locustopsidae.

In addition to the new taxa, we provide a taxonomic revision of several genera previously assigned to Locustopsidae. This includes the synonymizing of *Cratozeunerella* with *Zeunerella*, and *Plesioschwinzia* with *Locustopsis*, as well as the reallocation of multiple species to more appropriate genera such as *Mesolocustopsis*, *Schwinzia*, *Cratolocustopsis*, and *Locustopsis*. Furthermore, we clarify the status of problematic taxa such as *Sinolocustopsis* and recommend the exclusion of *Liadolocusta* and *Locustopsites* from Locustopsidae based on insufficient or contradictory morphological evidence.

Taken together, our findings reinforce the Crato Formation as a hotspot for caeliferan diversity during the Early Cretaceous and demonstrate the importance of rigorous morphological re-evaluation in fossil Orthoptera. The taxonomic refinements proposed herein lay the groundwork for future phylogenetic analyses of Locustopsidae and underscore the need for continued investigation of underexplored fossil insect assemblages in South America.

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References

Assine, M.L. (2007) Bacia do Araripe. *Boletim de Geociências da Petrobras*, 15, 371–389.

Assine, M.L., Perinotto, J.A.J., Neumann, V.H., Custódio, M.A., Varejão, F.G. & Mescolotti, P.C. (2014) Sequências Deposicionais do Andar Alagoas (Aptiano superior) da Bacia do Araripe, Nordeste do Brasil. *Boletim de Geociências da Petrobras*, 22 (1), 3–28.
https://doi.org/10.25249/0375-7536.1992289300

Assine, M.L., Quaglio, F., Warren, L.V. & Simões, M.G. (2016) Comments on paper by M. Arai, "Aptian/Albian (Early Cretaceous) paleogeography of the South Atlantic: a paleontological perspective". *Brazilian Journal of Geology*, 46, 3–7.
https://doi.org/10.1590/2317-4889201620150046A

Ander, K.E.V. (1939) *Vergleichend-anatomische und Phylogenetische studien über die Ensifera (Saltatoria). Vol. 2*. Berlingska Boktryckeriet, Lund. [unknown pagination]

Ansorge, J. (1991) Locustopsis africanus n. sp. (Saltatoria, Caelifera) aus der Unterkreide SW-Agyptens. *Neues Jahrb. Geol. Palaeontol. Monatsh.*, 1991 (4), 205–212.
https://doi.org/10.1127/njgpm/1991/1991/205

Arai, M. (2014) Aptian/Albian (Early Cretaceous) paleogeography of the South Atlantic: a paleontological perspective. *Brazilian Journal of Geology*, 44 (2), 339–350.
https://doi.org/10.5327/Z2317-4889201400020012

Arai, M. & Assine, M.L. (2020) Chronostratigraphic constraints and paleoenvironmental interpretation of the Romualdo Formation (Santana Group, Araripe Basin, Northeastern Brazil) based on palynology. *Cretaceous Research*, 116, 104610.
https://doi.org/10.1016/j.cretres.2020.104610

Béthoux, O. & Nel, A. (2002) Venation pattern and revision of Orthoptera sensu nov. and sister groups. Phylogeny of Palaeozoic and Mesozoic Orthoptera sensu nov. *Zootaxa*, 96 (1), 1–88.
https://doi.org/10.11646/zootaxa.96.1.1

Bezerra, F.I., da Silva, J.H., Miguel, E.C., Paschoal, A.R., Nascimento Jr., D.R., Freire, P.T.C., Viana, B.C. & Mendes, M. (2020) Chemical and mineral comparison of fossil insect cuticles from Crato Konservat Lagerstätte, Lower Cretaceous of Brazil. *Journal of Iberian Geology*, 46, 61–76.
https://doi.org/10.1007/s41513-020-00119-y

Bezerra, F.I., Solórzano-Kraemer, M.M. & Mendes, M. (2021) Distinct preservational pathways of insects from the Crato Formation, Lower Cretaceous of the Araripe Basin, Brazil. *Cretaceous Research*, 118, 104631.
https://doi.org/10.1016/j.cretres.2020.104631

Bezerra, F.I. & Mendes, M. (2024) A palaeoecological analysis of the Cretaceous (Aptian) insect fauna of the Crato Formation, Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 641, 112134.
https://doi.org/10.1016/j.palaeo.2024.112134

Bode, A. (1953) Die Insektenfauna des ostniedersächsischen oberen Lias. *Palaeontographica. Beitraege zur Naturgeschichte der Vorzeit*, 103, 1–375.

Brauer, F.M., Redtenbacher, J. & Ganglbauer, L. (1889) Fossile Insekten aus der Juraformation Ost-Sibiriens. *Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg*, 36, 1–22.

Brodie, P.B. (1845) *A history of the fossil insects in the secondary rocks of England*. J.van Voorst, London, 140 pp.
https://doi.org/10.5962/bhl.title.52321

Brullé, G.A. (1835) Cinquième Ordre. Orthoptères. *In*: *Histoire naturelle des insectes: Vol. 9 [1] (5)*. Société bibliophile, Paris, pp. 1–225. [225–416 in 1836]

Catto, B., Jahnert, R.J., Warren, L.V., Varejão, F.G. & Assine, M.L. (2016) The microbial nature of laminated limestones: lessons from the upper Aptian, Araripe Basin, Brazil. *Sedimentary Geology*, 341, 304–315.
https://doi.org/10.1016/j.sedgeo.2016.05.007

Cigliano, M.M., Braun, H., Eades, D.C. & Otte, D. (2025) Orthoptera Species File. Version July 2025. Available from: http://orthoptera.speciesfile.org/ (accessed 31 July 2025)

Cockerell, T.D.A. (1916) British fossil insects. *Proceedings of the United States National Museum*, 49, 469–499.
https://doi.org/10.5479/si.00963801.49-2119.469

Coimbra, J.C., Arai, M. & Carreño, A.L. (2002) Biostratigraphy of Lower Cretaceous microfossils from the Araripe basin, northeastern Brazil. *Geobios*, 35 (6), 687–698.
https://doi.org/10.1016/S0016-6995(02)00082-7

Coimbra, J.C. & Freire, T.M. (2021) Age of the Post-rift Sequence I from the Araripe Basin, Lower Cretaceous, NE Brazil: Implications for spatio-temporal correlation. *Revista Brasileira de Paleontologia*, 24 (1), 37–46. https://doi.org/10.4072/rbp.2021.1.03

Corecco, L., Bezerra, F.I., Silva Filho, W.F., Nascimento Jr., D.R., da Silva, J.H. & Felix, J.L. (2022) Petrological meaning of ethnostratigraphic units: Laminated Limestone of the Crato Formation, Araripe Basin, NE Brazil. *Pesquisas em Geociências*, 49 (1), e121139. https://doi.org/10.22456/1807-9806.121139

de Moura-Júnior, D.A., Scheffler, S.M. & Fernandes, A.C.S. (2018) A paleoentomofauna brasileira: cenário atual. *Anuário do Insituto de Geociências*, 41, 142–166. https://doi.org/10.11137/2018_1_142_166

Deichmüller, J.V. (1886) *Die Insecten aus dem lithographischen Schiefer in Dresdener Museum*. Fischer, Basel, 88 pp.

Dias, J.J. & Carvalho, I.D.S. (2022) The role of microbial mats in the exquisite preservation of Aptian insect fossils from the Crato Lagerstätte, Brazil. *Cretaceous Research*, 130, 105068. https://doi.org/10.1016/j.cretres.2021.105068

Geinitz, F.E. (1880) Der Jura von Dobbertin in Mecklenburg und seine Versteinerungen. *Zeitschrift der Deutschen Geologischen Gesellschaft*, 32, 510–535.

Germar, E.F. (1842) Beschreibung einiger neuen fossilen Insekten. I. in den lithographischen Schiefern von Bayern. II. Insektenflügel im Schieferthone des Steinkohlegebirges von Wettin. *Beiträge zur Petrefactenkunde*, 5, 79–94.

The GIMP Team (2025) GIMP. Version 3.0.2-1. Available from: https://www.gimp.org/ (accessed 7 October 2025)

Gorochov, A.V. (1985) Mesozoic crickets (Orthoptera, Grylloidea) of Asia [in Russian]. *Paleontologicheskiy Zhurnal*, 198 (2), 59–68.

Gorochov, A.V. (1995) System and evolution of the suborder Ensifera (Orthoptera). Part II. *Proceedings of the Zoological Institute of the Russian Academy of Sciences*, 260, 1–213.

Gorochov, A.V., Jarzembowski, E.A. & Coram, R.A. (2006) Grasshoppers and crickets (Insecta: Orthoptera) from the Lower Cretaceous of southern England. *Cretaceous Research*, 27 (5), 641–662. https://doi.org/10.1016/j.cretres.2006.03.007

Gorochov, A.V. & Coram, R.A. (2023) New and little known taxa of the order Orthoptera (Insecta) from the Upper Triassic and Lower Jurassic of England. *Palaeoentomology*, 6 (2), 198–204. https://doi.org/10.11646/palaeoentomology.6.2.11

Gu, J.J., Yue, Y., Shi, F.M., Tian, H. & Ren, D. (2016) First Jurassic grasshopper (Insecta, Caelifera) from China. *Zootaxa*, 4169 (2), 377–380. https://doi.org/10.11646/zootaxa.4169.2.9

Handlirsch, A. (1906) *Die fossilen Insekten und die Phylogenie der rezenten Formen: ein Handbuch für Paläontologen und Zoologen*. *Vol. 1.* W. Engelmann, Leipzig, IX + VI + 160 + XX + 672 + II + XII + II + II pp., XXXVI taf. https://doi.org/10.5962/bhl.title.5636

Handlirsch, A. (1939) Neue Untersuchungen über die fossilen Insekten mit Ergänzungen und Nachträgen sowie Ausblicken auf phylogenetische, palaeogeographische und allgemein biologische Probleme. II. Teil. *Annalen des naturhistorischen Museums in Wien*, 49, 1–240.

Heimhofer, U., Ariztegui, D., Lenniger, M., Hesselbo, S.P., Martill, D.M. & Rios-Neto, A.M. (2010) Deciphering the depositional environment of the laminated Crato fossil beds (Early Cretaceous, Araripe Basin, North-Eastern Brazil). *Sedimentology*, 57 (2), 677–694. https://doi.org/10.1111/j.1365-3091.2009.01114.x

Heimhofer, U. & Hochuli, P.A. (2010) Early Cretaceous angiosperm pollen from a low-latitude succession (Araripe Basin, NE Brazil). *Review of Palaeobotany and Palynology*, 161 (3–4), 105–126. https://doi.org/10.1016/j.revpalbo.2010.03.010

Hong Y.C. & Wang W.L. (1990) Fossil Insects from the Laiyang Basin, Shandong Province] *In*: Regional Geological Surveying Team, Shandong Bureau of Geology and Mineral Resources (Ed.), *The stratigraphy and Palaeontology of Laiyang Basin, Shandong Province*. Geological Publishing House, Beijing, pp. 44–189.

Kirby, W.F. (1906) Orthoptera Saltatoria. Part I. (Achetidae et Phasgonuridae). *In*: *A Synonymic Catalogue of Orthoptera (Orthoptera Saltatoria, Locustidae vel Acridiidae). Vol. 2.* British Museum (Natural History), London, pp. i–viii + 1–562.

Krauss, H.A. (1902) Die Namen der ältesten Dermapteren- (Orthopteren-) Gattungen und ihre Verwendung für Familien- und Unterfamilien-Benennungen auf Grund der jetzigen Nomenclaturregein. *Zoologischer Anzeiger*, 25 (676), 530–543.

Latreille, P.A. (1810) *Considérations générales sur l'ordre naturel des animaux composant les classes des Crustacés, des Arachnides, et des Insectes; avec un tableau méthodique de leurs genres, disposés en familles*. Chez F. Schoell, rue des Fosses S.G.l'Auxerrois, Paris, 444 pp. https://doi.org/10.5962/bhl.title.39620

Leach, W.E. (1815) Entomology. *In*: *The Edinburgh Encyclopaedia*. *Vol. 9.* William Blackwood, Edinburgh, pp. 57–172.

Lin, Q. (1982) Class Insecta. Shaanxi-Gansu-Ningxia volumn, Mesozoic and Cenozoic. *In*: *Paleontological atlas of Northwest China: Vol. II. Paleontological Atlas of Northwest China*. Geological Publishing House, Beijing, pp. 70–83.

Linnaeus, C. (1758) *Systema naturae*. *Vol. 1*. Laurentii Salvii, Stockholm, 824 pp.

Lúcio, T., Neto, J.A.S. & Selby, D. (2020) Late Barremian/early Aptian Re-Os age of the Ipubi Formation black shales:

Stratigraphic and paleoenvironmental implications for Araripe Basin, northeastern Brazil. *Journal of South American Earth Sciences*, 102, 102699.
https://doi.org/10.1016/j.jsames.2020.102699
MacLeay, W.S. (1821) *Horae Entomologicae or Essays on the Annulose Animals*. *Vol. 2.* S. Bagster, London. [unknown pagination]
Martill, D.M., Loveridge, R. & Heimhofer, U. (2007) Halite pseudomorphs in the Crato Formation (Early Cretaceous, Late Aptian–Early Albian), Araripe Basin, northeast Brazil: further evidence for hypersalinity. *Cretaceous Research*, 28, 613–620.
https://doi.org/10.1016/j.cretres.2006.10.003
Martins-Neto, R.G. (1990) The family Locustopsidae (Insects, Caelifera) in the Santana Formation (Lower Cretaceous, Northeast Brazil. I. Description of two new species of the genus Locustopsis Handlirsch and three new species of the genus *Zessinia* n. gen. *In*: *Atas do I Simposio sobre a Bacia do Araripe e bacias interiores do Nordeste*. DNPM, Crato, pp. 227–291.
Martins-Neto, R.G. (1995) Araripelocustidae, fam. n. uma familia de gafanhotos (Insecta, Caelifera) da Formação Santana, Cretáceo Inferior do nordeste do Brasil. *Revista Brasileira de Entomologia*, 39 (2), 311–319, illustr.
Martins-Neto, R.G. (1998) A new genus of the family Locustopsidae (Insecta, Caelifera) in the Santana Formation (Lower Cretaceous, northeastern Brazil). *Revista Española de Paleontologia*, 13 (2), 133–138.
https://doi.org/10.7203/sjp.24046
Martins-Neto, R.G. (2001) Review of some insects from Mesozoic and Cenozoic Brazilian deposits, with descriptions of new taxa. *Acta Geologica Leopoldensia*, 24 (52/53), 115–124.
Martins-Neto, R.G. (2003) Systematics of the Caelifera (Insecta, Orthopteroidea) from the Santana Formation, Araripe Basin (Lower Cretaceous, northeast Brazil), with a description of new genera and species. *Acta Zoologica Cracoviensia*, 46, 205–228.
Martynov, A.V. (1937) Liasovyye nasekomyye Shuraba i Kizil-Kii (Liassic Insects of Shurab and Kizyl-Kiya). *Trudy Paleontologicheskogo Instituta, Akademiia Nauk SSSR [Transactions of the Institute of Paleontology, USSR Academy of Sciences]*, 7 (1), 5–232.
Melo, R.M., Guzmán, J., Almeida-Lima, D., Piovesan, E.K., Neumann, V.H.D.M.L. & Sousa, A.D.J.E. (2020) New marine data and age accuracy of the Romualdo Formation, Araripe Basin, Brazil. *Scientific Reports*, 10 (1), 15779.
https://doi.org/10.1038/s41598-020-72789-8
Mendes, M., Vasconcelos, S.M.O.L. de & Oliveira, F.I.B. de(2019) A new fossil stick grasshopper (Proscopioidea: Proscopiidae) from the Crato formation of Brazil. *Anuário do Instituto de Geociências, UFRJ*, 42 (2), 437–443.
https://doi.org/10.11137/2019_2_437_443
Mendes, M., Bezerra, F.I. & Adami, K. (2020) Ecosystem Structure and Trophic Network in the Late Early Cretaceous Crato Biome. *In*: Iannuzzi, R., Rößler, R. & Kunzmann, L. (Eds.), *Brazilian Paleofloras: from Paleozoic to Holocene*. Springer, Cham, pp. 1–19.
https://doi.org/10.1007/978-3-319-90913-4_33-1
The Inkscape Team (2025) Inkcape. Version 1.4.2. Available from: https://inkscape.org/de/ (accessed 31 July 2025)
Nel, A. & Jouault, C. (2022) New grasshoppers (Orthoptera: Elcanidae, Locustopsidae) from the Lower Cretaceous Crato formation suggest a biome homogeneity in Central Gondwana. *Historical Biology*, 34 (10), 2070–2078.
https://doi.org/10.1080/08912963.2021.2000602
Nel, A. & Huang, D.Y. (2024) New locustopsid fossils from the Middle Jurassic Yan'an Formation (Orthoptera: Caelifera). *Journal of Insect Biodiversity*, 60 (1), 16–23.
Neumann, V.H., Borrego, A.G., Cabrera, L. & Dino, R. (2003) Organic matter composition and distribution through the Aptian–Albian lacustrine sequences of the Araripe Basin, northeastern Brazil. *International Journal of Coal Geology*, 54 (1–2), 21–40.
https://doi.org/10.1016/S0166-5162(03)00018-1
Ponte, F.C. & Ponte-Filho, F.C. (1996) *Estrutura geológica e evolução tectônica da Bacia do Araripe*. Departamento Nacional de Produção Mineral, Recife, 68 pp.
Santos, F.H., Azevedo, J.M., Nascimento Jr., D.R., Souza, A.C.B., Mendes, M., Bezerra, F.I. & Limaverde, S. (2017) Análise de fácies e petrografia de uma seção do Membro Crato em Nova Olinda (CE): contribuições à história deposicional e diagenética do neoaptiano na Bacia do Araripe. *Geologia*, Série Científica, 17 (1), 3–18.
https://doi.org/10.11606/issn.2316-9095.v17-319
Serville, J.G.A. (1838) *Histoire naturelle des insectes. Orthoptères*. Librairie Encyclopédique de Roret, Paris, xviii + 776 pp., 14 pls. [1839]
Sharov, A.G. (1968) Filogniya orthopteroidnykh nasekomykh [1971 English translation: Phylogeny of the Orthopteroidea]. *Trudy Paleontologicheskogo Instituta, Akademiia Nauk SSSR [Transactions of the Institute of Paleontology, USSR Academy of Sciences]*, 118, 1–216.
Smith, D.M., Gorman, M.A., Pardo, J.D. & Small, B.J. (2011) First fossil Orthoptera from the Jurassic of North America. *Journal of Paleontology*, 85 (1), 102–105.
https://doi.org/10.1666/10-096.1
Strand, E. (1926) Miscellanea nomenclatorica zoologica et palaeontologica. *Archiv für Naturgeschichte*, 92 (8), 30–75. [1928]
The Paleobiology Database (2025) The Paleobiology Database. Available from: https://paleobiodb.org/#/ (accessed 15 August 2025)

Théobald, N. (1937) *Les Insectes Fossiles des terrains oligocenes de France*. Imprimerie Georges Thomas, Angle des rues de Solignac et Henri-Lepage, Nancy, 473 pp.
von Laicharting, J.N.E. (1781) *Verzeichnis und Beschreibung der Tyroler Insecten*. *Vol. 1*. bey J.C. Füessly, Zürich, XII + 176 pp.
Whalley, P.E.S. (1985) The systematics and palaeogeography of the Lower Jurassic insects of Dorset, England. *Bulletin of the British Museum (Natural History) Geology*, 39 (3), 107–189.
Zessin, W. (1983) Revision der mesozoischen Familie Locustopsidae unter Berücksichtigung neuer Funde (Orthopteroida, Caelifera). *Deutsche Entomologische Zeitschrift*, 30 (1–3), 173–237. https://doi.org/10.1002/mmnd.19830300115
Zessin, W. (1983) Locustopsis kruegeri n. sp. (Orthopteroida, Caelifera) aus dem oberen Lias von Schandelah bei Braunschweig (BRD). *Zeitschrift für geologische Wissenschaften*, 11 (7), 905–910.
Zessin, W. (1988) Neue Saltatoria (Insecta) aus dem Oberlias Mitteleuropas. *Freiberger Forschungshefte*, Reihe C, 419, 107–121.
Zeuner, F.E. (1942) The Locustopseidae and the phylogeny of the Acridodea (Orthoptera). *Proceedings of the Royal Entomological Society of London*, Series B, 11 (1), 1–19. https://doi.org/10.1111/j.1365-3113.1942.tb00713.x
Zherikhin, V.V. (1985) Jurassic orthopterans of south Siberia and western Mongolia. *Trudy Paleontologicheskogo Instituta, Akademiia Nauk SSSR [Transactions of the Institute of Paleontology, USSR Academy of Sciences]*, 211, 171–184.